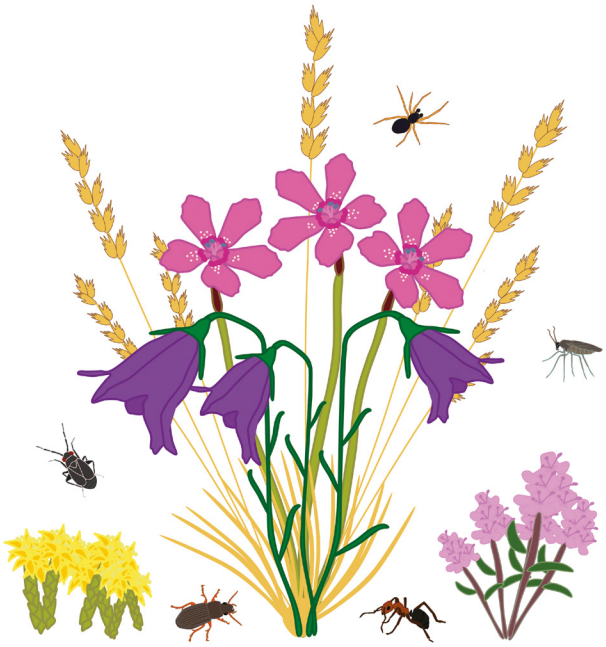
Vegetated roofs as habitats for arthropods in urban areas

KUKKA KYRÖ



Faculty of Biological and Environmental Sciences
University of Helsinki
2021

VEGETATED ROOFS AS HABITATS FOR ARTHROPODS IN URBAN AREAS

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ACADEMIC DISSERTATION

To be presented for public examination with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki in the lecture hall 108 in Metsätieteiden talo (Latokartanonkaari 7) on the 13th of August 2021 at 1pm.

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ISBN 978-951-51-7424-6 (paperback)
ISBN 978-951-51-7425-3 (PDF)
http://ethesis.helsinki.fi
Painosalama
Turku 2021

Nosta jalka kaasulta:
perhonen ylittää tien.

Eeva Kilpi

Contents

Original articles

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I Kyrö K, Brenneisen S, Kotze DJ, Szallies A, Gerner M, Lehvävirta S (2018) Local habitat characteristics have a stronger effect than the surrounding urban landscape on beetle communities on green roofs. Urban Forestry & Urban Greening 29:122–130. https://doi.org/10.1016/j.ufug.2017.11.009

II Kyrö K, Kotze DJ, Müllner MA, Hakala S, Kondorosy E, Pajunen T, Vilisics F, Lehvävirta S (2020) Vegetated roofs in boreal climate support mobile open habitat arthropods, with differentiation between meadow and succulent roofs. Urban Ecosystems 23:1239-1252. https://doi.org/10.1007/s11252-020-00978-4

III Kyrö K, Kankaanpää T, Vesterinen EJ, Lehvävirta S, Kotze DJ (2021) Arthropod communities on young vegetated roofs are more similar to each other than to communities at ground level. Manuscript

Table of contributions

	I	II	III
Original idea	SB, KK, SL	FV, KK, SL	SL, KK
Study design	SB, KK, SL	FV, KK, SL	KK, SL
Data collection	SB, MG	KK, FV, MM, SL	KK, JK, SL
Arthropod species identification	AS	SH, EK, TP	KK, TK, EV
Data analyses	KK, SL, JK	KK, JK, SL	KK, TK, JK, EV, SL
Manuscript preparation	KK, SL, JK, SB, MG, AS	KK, SL, JK, SH, EK, MM, FV, TP	KK, JK, TK, SL, EV

AS = Alexander Szallies, EK = Előd Kondorosy, EV = Eero Vesterinen, FV = Ferenc Vilisics, JK = Johan Kotze, MG = Magda Gerner, MM = Malgorzata Müllner, KK = Kukka Kyrö, SB = Stephan Brenneisen, SH = Sanja Hakala, SL = Susanna Lehvävirta, TK = Tuomas Kankaanpää, TP = Timo Pajunen

ABSTRACT

Urbanisation drives drastic changes in land cover and land use with multiple environmental impacts. A compact city structure, e.g., helps to reduce energy consumption and fossil fuel emissions. Yet, the increase in urbanized land cover has become a major cause of habitat loss and fragmentation – factors that are rated among the greatest threats to the variety of life on earth. Thus, there is an urgent call to search for tools that mitigate and, eventually, halt the decline of wildlife and plants with urbanization.

In this thesis, I study vegetated roofs as tools for arthropod conservation in urban environments. Vegetated roofs, also known as green roofs, are purposely covered with substrate or soil and plants. They avert a multitude of environmental problems caused by the replacement of natural habitats with anthropogenic land use. They can be used, e.g., for stormwater retention and carbon sequestration. In addition, they turn building tops into habitat for plants and mobile animals. Thus, they are assumed to mitigate the loss of habitat and biodiversity due to urban development, but knowledge from vegetated roofs as habitat patches has not been sufficient to evaluate this assumption.

I use arthropod data from vegetated roofs with low-growing, drought tolerant vegetation dominated either by forbs and/or grasses or succulents and mosses. I describe arthropod assemblages (beetles in **Chapter I** and multi taxa assemblages in **Chapters II & III**) using taxonomic and trait data and apply island biogeography theory and community ecology as frameworks to study the effects of biophysical roof characteristics, roof age and the landscape on arthropod abundance, richness and community composition.

I found vegetated roofs to host arthropods with active and passive aerial dispersal strategies and either tolerating a wide range of habitats or associated with dry habitats. Most species were common generalists, but a few rare and endangered species also occurred on roofs. In addition, I found indication that vegetated roofs may sometimes serve as platforms for introductions of exotic arthropod species. Both local roof characteristics and the landscape shaped arthropod community composition on vegetated roofs. Roof characteristics, particularly vegetation, but also roof height and age, shaped arthropod abundance with taxon-specific effects. Most taxa responded positively to forb cover or to a combined cover of forbs and grasses, and some phytophagous groups were rare on roofs that had vegetation consisting almost exclusively of succulents and mosses. The vertical isolation of roof habitats is an effective filter that excludes less mobile species, but species that were able to colonize the roofs responded even positively to roof height, possibly because of decreased competition and/or predation. Roof age had a variable effect on arthropod abundance and richness, which are likely connected to variation in the vegetation and changes in biotic interactions.

In this thesis, I have shown that urban vegetated roofs with shallow substrate benefit native arthropods associated with dry habitats and open vegetation, but do not automatically provide high biodiversity values and may sometimes serve as agents for exotic species. The ecological value of roofs can be improved by designing them from a habitat provision perspective and as part of the habitat network existing at ground level. My results point to the benefits of planting roofs with diverse vegetation instead of using only a few succulent species, when designing vegetated roofs to support a rich arthropod fauna.

SUMMARY

1 INTRODUCTION

1.1 URBANIZATION THREATENS BIODIVERSITY, BUT THERE IS MORE TO THE STORY

Increasing urbanization is a global megatrend and a key driver of anthropogenic landscape change (Grimm *et al.* 2008; Retief *et al.* 2016). Given that the growth of urban areas means the replacement of natural habitats with roads, buildings, parking lots and other artificial non-vegetated surfaces, the effects of urban development on wildlife are typically negative (Aronson *et al.* 2014; Piano *et al.* 2020b), and urbanization, particularly as a cause for habitat loss, is rated among the greatest global threats to biodiversity (McDonald *et al.* 2020). Yet, research on urban biodiversity assessments show that not all patterns related to urbanization are harmful to wildlife (McKinney 2008; Ives *et al.* 2016), and urban development creates important possibilities for nature conservation (Dearborn and Kark 2010; Aronson *et al.* 2017; Ossola and Niemelä 2018; Soanes *et al.* 2019). For example, high habitat heterogeneity is typical of urban areas and often positively linked with species richness (Sattler *et al.* 2010). Also, some flower-visiting insects may benefit from urbanization because of increased availability of floral resources and reduced use of pesticides in cities compared to rural areas (Theodorou *et al.* 2020). Seizing conservation opportunities in urban environments and enhancing urban biodiversity is critical, not only for wildlife, but also for humans, as exposure to nature is an essential component of our health and wellbeing (Tzoulas *et al.* 2007; Russell *et al.* 2013; Haahtela 2019).

The protection of relatively large continuous green spaces within urban areas, i.e. land sparing, is recognized as essential to support a rich urban flora and fauna and to sustain important ecosystem services (Stott *et al.* 2015; Gallo *et al.* 2017). Yet, growing cities face an enormous challenge in balancing between maintaining ground level green space and attaining societal and environmental benefits from compact development (Haaland and van den Bosch 2015). Thus, approaches encouraging environmentally sustainable urbanization, such as nature-based solutions (NBS) – a concept promoted by the European Commission that applies solutions inspired and supported by nature to provide environmental, social and economic benefits and increase resilience of societies (Maes and Jacobs 2017) – promote developing also solutions, where ground-level green space is complemented by vegetation that is integrated into buildings, and particularly on roofs, i.e. intense land-sharing.

*1.2 VEGETATED ROOFS: COULD WILDLIFE THRIVE **ON** A CITY?*

Vegetated roofs, also known as green roofs (but see Kotze *et al.* 2020), are roofs with purposely established vegetation cover. They vary from lush garden-like constructions to roofs covered with mosses, succulents or other drought tolerant species growing on thin substrates. In my work, I focus on roofs that have low-growing vegetation consisting of forbs, grasses, succulents and mosses (Fig. 1). They are designed to function as nearly self-sustaining ecosystems, and do not require frequent irrigation or fertilization. Low maintenance vegetated roofs have rapidly become popular in large cities as NBS that help to support a variety of ecosystem services in dense urban areas while creating little maintenance costs (Oberndorfer *et al.* 2007; Nurmi *et*

al. 2016). These kinds of roofs mimic open dry environments, such as dry and rocky meadows (Lundholm and Marlin 2006) – habitats that, during the past century, have steeply declined in rural areas in Finland and elsewhere in Europe (Fuller 1987; Riley 2005; Kontula and Raunio 2018).

As vegetated roofs integrate habitats into building envelopes, they provide an intriguing opportunity to support wildlife, particularly arthropods and other invertebrates, even in urban cores. Theoretically, roofs with vegetation cover relate to six of the seven ecological principles recognized by Parris *et al.* (2018) to play a critical role in promoting biological conservation in urban areas: they increase *connectivity* of urban green space, are *constructed ecosystems* that can be designed to enhance habitat diversity, they participate in sustaining *ecosystem cycles* (e.g. water cycle), support and re-establish *ecological interactions*, are intended to be *benevolent structures* for wildlife, and are ecosystems that comprise of novel human-designed species assemblages. Accordingly, vegetated roofs are expected to have high conservation potential, but the realized value of vegetated roofs for urban nature remains unclear (Williams *et al.* 2014; MacIvor and Ksiazek 2015).

Conservation benefits of vegetated roofs are constrained by social, cultural and economic aspects that often overrule cherishing diverse communities of native species (Aronson *et al.* 2017). Thus, species-rich plant assemblages that resemble local natural and semi-natural habitats may not be the main objective in roof design (Williams *et al.* 2014). In the absence of guidelines and regulation that ensure that conservation aspects are taken into account, a common procedure is to plant roofs with a couple of drought tolerant stonecrop species (Gabrych *et al.* 2016), and the resulting low plant diversity is likely to limit the value of vegetated roofs as habitat for invertebrates (Haddad *et al.* 2009). Also, many roofs are planted with non-natives and plant material that is imported from abroad. Because international horticultural trade is an important source of invertebrate invasions (Kenis *et al.* 2007), such vegetated roofs form a potential source for introductions of non-native invertebrate species (Kadas 2006; Páll-Gergely *et al.* 2014). Finally, even roofs that are particularly designed to support local plant and animal populations and, e.g., have variation in substrate depth and material, and are planted with diverse native vegetation, may eventually fail to meet the target because vertical isolation, small size and a harsh microclimate of the roofs, including continuous exposure to strong winds and scorching heat, can

Figure 1. Examples of vegetated roofs included in this study: meadow roofs, where vegetation is dominated by forbs and grasses (a, b), succulent roofs with vegetation consisting almost solely of succulents and mosses (c, d).

limit their utility for wildlife (Williams *et al.* 2014). Furthermore, there is a risk that vegetated roofs function as sink habitats by receiving passive dispersers and even attracting actively dispersing species that fail to persist on roofs due to unsuitable environmental conditions (MacIvor and Ksiazek 2015; Rumble *et al.* 2018). In such situations vegetated roof communities would rely on constant recolonization from sources at ground level or from other vegetated roofs with functional habitat.

1.3 VEGETATED ROOFS AS ARTHROPOD HABITATS

Arthropods have rapidly become a focal animal group in research on biodiversity value of vegetated roofs (Filazzola *et al.* 2019). Because arthropods are small and generally mobile organisms, they are likely to benefit even from isolated and small roof habitats. Indeed, the first surveys on arthropod fauna on vegetated roofs pointed to high conservation potential: they highlighted findings of rare and endangered stenotopic species and boosted ideas of applying vegetated roofs as conservation tools (Jones 2002; Kaupp *et al.* 2004; Brenneisen 2006; Brenneisen and Hänggi 2006; Kadas 2006).

When I started this thesis, knowledge on vegetated roof fauna was based almost exclusively on faunistic surveys using no or simple descriptive statistics and lacking implementation of observations to ecological theory. With time, however, studies on vegetated roof arthropods have started to integrate community and landscape ecology and island biogeography as theoretical frameworks to search for generalizable ecological patterns and a mechanistic understanding of these patterns (Madre *et al.* 2013; Braaker *et al.* 2014, 2017; Blank *et al.* 2017; Ksiazek-Mikenas *et al.* 2018). The geographic coverage and taxonomic scope of research in this field have remained narrow, concentrating on areas with a temperate climate, considering one or a few taxa and focusing often on the same arthropod groups: beetles (Coleoptera), particularly carabids (Carabidae), spiders (Araneae) and bees (Hymenoptera: Aculeata: Apoidea). Research including a wider variety of arthropods typically apply data with low taxonomic resolution, and, hence, provides coarse information on community and diversity patterns. Furthermore, trait data can significantly increase our understanding of ecological features of roof communities (Gagic *et al.* 2015), and while several studies include some information on species traits, such as dispersal ability or habitat affinity, to describe the characteristics of roof fauna (Kaupp *et al.* 2004; Madre *et al.* 2013; Pétremand *et al.* 2018; Bergeron *et al.* 2018), research on the response of species traits to environmental gradients of roofs are still rare (but see Braaker *et al.* 2017).

Overall, research on mechanisms shaping arthropod communities on vegetated roofs has only started to step out of its infancy, and study designs that allow modelling of species and/or community responses to spatial, temporal, environmental or biotic features are still rare. Yet, assessing the potential and limitations of vegetated roofs as tools for arthropod conservation and developing guidelines for practitioners requires understanding of mechanisms that shape arthropod assemblages in these novel habitats (Simberloff 2004; Williams *et al.* 2014).

1.3.1 Islands in a sea of concrete

Ecologically, urban vegetated roofs are considered to function as islands distributed within a matrix that is heterogeneous but characterized by a high coverage of impervious surfaces. Thus, the classical island biogeography theory (IBT) (MacArthur and Wilson 1967) provides a possibly valuable framework for hypotheses on species richness in roof habitats. IBT predicts diversity as a dynamic equilibrium of immigration and extinction, which depend on island or habitat patch size and connectivity to source habitats. Accordingly, species richness should increase with roof size and decrease with isolation to source habitats.

Species richness patterns observed in habitat patches that are not oceanic islands result from more complex spatial and temporal processes (Rosenzweig 1995; Brown and Lomolino

2000). Regarding roofs, habitat quality, typically described as vegetation and substrate characteristics, is expected to be a particularly important feature in explaining arthropod species richness. Also, because the urban matrix is heterogeneous and less hostile than the ocean matrix in the original IBT, its effects may not be only negative. Another complication to predictions derived from IBT is the typically small size of "roof islands": the small-island effect hypothesis (SIE) states that there is a breakpoint in island area below which variation in species richness is no longer connected to island size (Lomolino 2000). Finally, unlike young oceanic islands, vegetated roofs are quickly covered with vegetation, which may have an effect on the colonization process of arthropods.

1.3.2 Arthropod community assembly on vegetated roofs

Species richness patterns provide one viewpoint for evaluating vegetated roofs as arthropod habitats. Another important aspect is species identity, i.e., community assembly. In biological communities, dispersal constraints, the abiotic environment and biotic interactions assemble communities, together with random processes (Zobel 1997; Leibold *et al.* 2004; Götzenberger *et al.* 2012). In the case of vegetated roofs and other engineered habitats, filtering effects of dispersal constraints, and abiotic and biotic processes modulated by human decisions, are particularly interesting. Vegetated roofs are designed to fit for purpose, such as landscaping, stormwater management, recreation, biological conservation or their combination (Kotze *et al.* 2020). Thus, it is important to know to what extent design is connected to the outcome.

To investigate the role of roofs' biophysical characteristics on biodiversity benefits described as abundance and richness of arthropods and features of community composition, I first identified roof characteristics potentially important in shaping the roof arthropod fauna (Fig. 2). Dispersal constraints of roof habitats comprise of building height and horizontal distance to ground level habitats and to other vegetated roofs. Horizontal distance to source habitats sets a dispersal barrier that acts at the regional scale (Braaker *et al.* 2014) and vertical isolation may prevent even local species, especially flightless ones, from establishing on roofs. Furthermore, roof height is not only a measure of connectivity, but it also affects microclimate on the roof (Walker 2011), a likely important abiotic filter. Strong winds and little to no chances to escape the scorching sun are typical conditions of high roofs, while low roofs are less windy and more likely to be shaded by surrounding buildings or trees. Another potentially important filter is the substrate, which may affect arthropods both directly (Boulton *et al.* 2005) and indirectly via its effects on vegetation (Olly *et al.* 2011). For example, the combination of a thin substrate and a lack of irrigation creates frequent droughts (Berretta *et al.* 2014) affecting arthropods directly and indirectly by exposing plants to high stress levels with consequent, community level, effects on arthropods (Trotter *et al.* 2007; Prather *et al.* 2020).

Vegetation is a key component of roof design and an important driver of arthropod diversity, abundance and community composition (Siemann *et al.* 1998). Plants set a biotic filter for herbivores with a strength that increases with increase in the level of specialization of the herbivore (Price 2002). Vegetation also affects predatory arthropods directly, as vegetation structure is an important component of their physical environment (Langellotto and Denno 2004; Gómez *et al.* 2016), and indirectly via bottom-up effects through their herbivorous prey species (Siemann *et al.* 1998; Haddad *et al.* 2009). Finally, biotic interactions between arthropods, i.e. competition, predation and mutualism, are likely important, but difficult to detect and disentangle from other assembly processes (Kraft *et al.* 2015; Cadotte and Tucker 2017). Thus, their role is typically omitted.

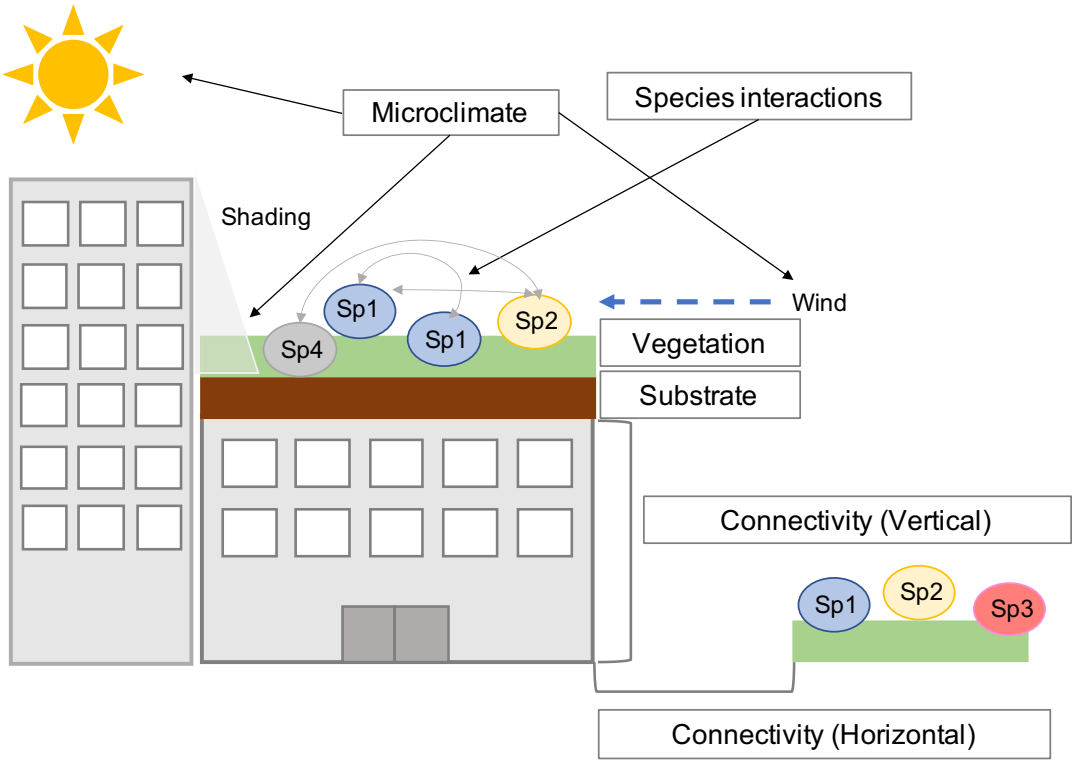

Figure 2. Environmental, biotic and dispersal filters contributing to community assembly of arthropods on vegetated roofs. Sp = Arthropod species. Sp4 is either introduced via roof construction materials or colonizes roofs from a regional species pool.

1.3.3 Colonization of new vegetated roofs: who arrives first and how? Does it matter?

Vegetated roofs provide a rare opportunity to follow colonization of new habitats. Unlike habitat patches generated via fragmentation, new roofs lack a historical connection to the surrounding landscape. Because substrates and plant materials carry arthropods, the first bits of the roof fauna are formed already during the construction phase (Páll-Gergely *et al.* 2014; Rumble *et al.* 2018; McKinney *et al.* 2019). After establishment, arthropods start arriving on vegetated roofs mainly by actively flying or via passive aerial dispersal (Colla *et al.* 2009; MacIvor and Lundholm 2011; Braaker *et al.* 2014; Vergnes *et al.* 2017), but details on arthropod colonization and the assembly of communities on new roofs are not known.

As the order of species arrival, i.e. historical contingency, can drive the outcome of community assembly via priority effects (Chase 2003; Fukami 2015), knowledge of the pioneer arthropod fauna of vegetated roofs may be critical to understand community patterns on older roofs and mechanisms driving them. In fact, Ksiazek-Mikenas *et al.* (2018) suggested priority effects as a likely explanation for the observed uniqueness of community composition of vegetated roofs in their space-for-time substitution study, which highlights the need for descriptions of pioneer species and their source habitats.

1.3.4 Filtering of arthropod traits

The inclusion of species trait data, i.e., body size, dispersal mode and feeding group, allows for the linking of species responses to their ecology. Thus, information on species traits can reveal mechanisms behind observed community patterns (McGill *et al.* 2006; Cadotte *et al.* 2015; Moretti *et al.* 2017). The arthropod communities of urban environments are filtered through a set of hierarchical filters that include biogeography and climate, land use and human facilitation (e.g. introductions of non-native species) (Aronson *et al.* 2016; Fournier *et al.* 2020). In addition to these filters, features that are typical for urban environments regardless of their location, such as high level of habitat fragmentation, prevalence of impervious surfaces and higher temperatures compared to surrounding rural areas, shape the urban species pool. In general, urban filters favours mobile, disturbance- and heat-tolerant generalist species, while sensitive specialists and species with low mobility are most vulnerable to urbanization (McKinney 2006; Menke *et al.* 2011; Burkman and Gardiner 2014; Piano *et al.* 2017, 2020a; Fournier *et al.* 2020; Franzén *et al.* 2020).

The roof habitat still sets an additional environmental and dispersal filter on top of an urban filter. Therefore, traits of the vegetated roof arthropod fauna should present a subset of the urban ground level fauna, but the strength of the additional environmental and dispersal filters are inadequately understood. Are arthropods inhabiting urban ground level green space sufficiently mobile and tolerant to occupy vegetated roofs, or do roof communities consist of the most mobile and tolerant component of the potential source fauna? Furthermore, do specialist species spontaneously find their way and establish on the roofs if suitable conditions are offered, and can poorly dispersing species, which may already be rare in the urban species pool, find their way onto the roofs? To be able to answer these questions, we need information on species traits across various taxa.

2 AIMS OF THE STUDY

The overall aims of my work are to evaluate the contribution of minimal maintenance vegetated roofs as arthropod habitats in the urban environment and to search for roof characteristics that promote a rich arthropod fauna. I study patterns in vegetated roof arthropod fauna and apply IBT and assembly theories in community ecology to connect the observed patterns with potential processes and mechanisms behind them. I investigate how arthropod abundance, richness and community composition are connected to local biological and physical roof characteristics, to roof age, and to the urban landscape. In addition, I describe arthropod fauna of newly established roofs and follow temporal patterns in these pioneer communities, with reference to adjacent ground level green space. I evaluate the roles of stochastic and deterministic processes in explaining the observed patterns in community assembly on the new roofs.

My main questions include:

- How do local biophysical roof characteristics and roof age affect arthropod richness, abundance, occurrence and community composition? (**I–III**)
- Do characteristics of the vegetated roof arthropod fauna differ between different climates? (**I–III**)
- What is the role of the surrounding landscape in shaping arthropod richness, abundance and community composition on urban vegetated roofs? (**I**)
- Do vegetated roofs with drought-tolerant vegetation support arthropod species associated with xeric habitats? (**I–III**)
- What are the roles of stochastic and deterministic processes in explaining patterns in arthropod community assembly of young vegetated roofs? (**III**)

3 MATERIAL AND METHODS

3.1 STUDY AREA

In **Chapter I**, I used beetle data collected from the city of Basel, Switzerland (47°34'N, 7°36'E). The multi-taxa data collected for **Chapters II and III** are from Helsinki, Finland (60°10'N, 24°56'E), with a few of the study roofs located also in the larger Helsinki capital region. Basel has a milder climate compared to Helsinki that locates at the northern edge of the hemi-boreal region. Basel is among the world's pioneer cities in vegetated roof building with 23% of flat roofs having vegetation cover already in 2006 (Kazmierczak and Carter 2010). In Helsinki, the area covered by vegetated roofs is low (ca. 4 ha in 2013) but new vegetated roofs are being built with an accelerating pace and in 2016 the city of Helsinki set a strategy to promote the building of vegetated roofs (Helsingin kaupunki 2016).

3.2 ARTHROPOD DATA

3.2.1 Field sampling

Arthropod data were collected from vegetated roofs (**I–III**) and urban ground level habitats of roughly equivalent type (**III**) using two sampling methods: pitfall traps (**I**) and vacuum sampling (**II and III**) (Fig. 3). Pitfall traps are commonly applied to study arthropods in ground level habitats (Greenslade 1964), and they have also been popular in vegetated roof arthropod surveys (Brenneisen and Hänggi 2006; Madre *et al.* 2013; Braaker *et al.* 2017; Pétremand *et al.* 2018). However, on roofs with very shallow substrates or on roofs established with prefabricated vegetation mats, which have synthetic fibres to keep the mat together, it is difficult or even impossible to make proper-sized holes for pitfall traps. Therefore, I chose vacuum sampling as an arthropod collection method in **Chapters II and III**. Vacuum sampling is efficient in capturing small and light epigaeic arthropods, while it may miss large and heavy arthropods, species that cling to the vegetation and those that hide under stones or in

Figure 3. Arthropod data for the thesis were collected using pitfall traps (on the left, **Chapter I**, Photo: Lieve Dierckx) and a D-vac vacuum sampling device (on the right, **Chapters II & III**).

the substrate (Mommertz *et al.* 1996). Also, data from vacuum sampling presents only a snapshot of the fauna, whereas pitfall traps can be placed on roofs over long time periods, and thus, give a more holistic picture of the roof fauna. To decrease data limitations from snapshot sampling, several vacuum collections were conducted per growing season (**II and III**).

3.2.2 Identifications

Arthropods were identified from morphological features for **Chapters I and II** by experts of each taxon. In **Chapter I**, all collected beetles were identified to species level. In **Chapter II**, spiders, true bugs (Hemiptera: Heteroptera) and ants (Hymenoptera: Apocrita: Formicidae) were identified to species. For the rest of the arthropod data in **Chapter II**, I applied order and suborder identifications. For **Chapter III**, I applied COI DNA metabarcoding (Hebert *et al.* 2003) with the Barcode of Life Data System (BOLD) as a reference library to identify arthropod samples.

3.2.3 Trait data

In **Chapter II**, I used arthropod trait data including body size, feeding-related features, dispersal and habitat affinity to identify and describe typical arthropod traits on vegetated roofs. The original aim was to further evaluate connections between species traits and roof characteristics, but the power of statistical analyses with trait data turned out to be too low. Thus, the results were unreliable, and I decided to use trait data only for descriptive purposes. In **Chapter III**, the taxonomic scope was too wide to include comprehensive trait data, as trait databases are still lacking for most arthropod groups. However, I applied information on larva/juvenile feeding groups to account for a (narrow) trait aspect in arthropod community assembly on newly established vegetated roofs.

3.3 ROOF CHARACTERISTICS

To investigate effects of the local environment on arthropod richness, abundance, occurrence and community composition, I identified roof characteristics that may be important for arthropod immigration, emigration, survival and reproduction. These roof characteristics included roof height and size, covers of forbs and grasses, substrate depth, number of plant species, dead plant material, total vegetation cover and roof age. Data limitations and collinearity among variables prevented me from combining all potentially important roof characteristics in the models. Therefore, I applied different variable combinations when modelling arthropod parameter responses to roof characteristics in **Chapters I, II and III**.

3.4 LANDSCAPE

In **Chapter I**, I inspected responses of the fauna to landscape characteristics to evaluate the role of regional land use in shaping roof communities. I applied land use data to describe landscape structure in the immediate surroundings of the studied roofs (100 m radius) and of a larger area (400 m radius) and assigned each land use class as potential source habitat or likely non-habitat to inspect relationships between beetle abundance, richness and community composition and landscape composition (Fig. 4). Open and semi-open green space was considered as potential source habitat while impervious surface, water and forest were deemed likely non-habitats for species establishing populations on roofs. Buildings were hypothesized to be habitats or non-habitats, depending on whether or not they had vegetated roofs.

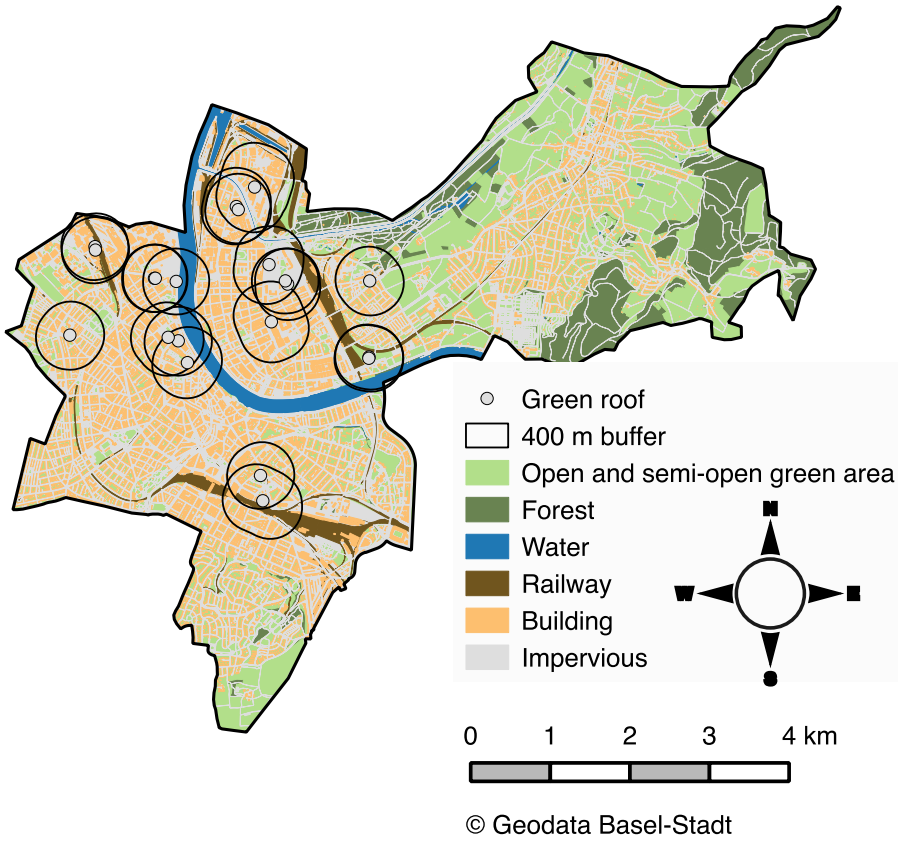

Figure 4. Locations of the studied vegetated roofs in Chapter I with 400 m buffer zones surrounding the roofs and land use data showing landscape composition in the city of Basel.

3.5 DATA ANALYSES

3.5.1 Single taxon models and diversity metrics analyses

I modelled single taxon responses to local roof characteristics (**I & II**) and landscape properties (**I**). Starting from individual species, but applicable to higher taxa as well when data were too few for species-specific analyses, I investigated dependencies between arthropod abundance and roof characteristics and land use variables with generalized linear mixed models (GLMMs). I also applied GLMMs to species richness with the same explanatory variables as in single taxon models to investigate how roof and landscape characteristics were connected to numbers of species on the roofs. I evaluated the importance of the variables in shaping arthropod communities based on the frequency of each variable to appear in the final models after model selection, which was based on AIC/AICc- and p-values. I used information on the direction and variation in response trends to provide guidelines for roof designs that promote a rich arthropod fauna, while refrained from taxon-specific recommendations, because multiple testing increased the probability for Type I errors for individual models, and because models for higher taxa (genus, family, suborder, order) combined potentially varying responses of multiple species.

3.5.2 Detecting community patterns from ordinations

I linked arthropod community composition with environmental variables using non-metric multidimensional scaling (NMDS). NMDS is an unconstrained ordination method that applies rank information to organize multivariate community data along a reduced number of axes representing main variation trends in the data (Legendre and Legendre 2012). NMDS accounts for non-linear responses and provides an easy visualization of patterns in community data. The NMDS axes can further be connected with environmental gradients for statistical testing of research hypotheses on the relationships between environmental variables and community composition.

3.5.3 Joint species distribution models

In **Chapter III**, I applied joint species distribution models (JSDMs) to model community responses to environmental filters (i.e. roof characteristics) that were considered potentially important for community assembly. JSDMs connect independently modelled taxa into one model in a way that accounts for correlations between species and assumes shared responses for similar species: e.g. species sharing traits are assumed to respond similarly to environmental gradients (Warton *et al.* 2015). I chose hierarchical modelling of species communities (HMSC), which is a method based on hierarchical Bayesian generalized linear mixed models (Ovaskainen and Soininen 2011; Ovaskainen *et al.* 2017; Ovaskainen and Abrego 2020), as a statistical framework for JSDMs. HMSC is a computationally efficient method that allows combining community data to spatio-temporal, environmental, phylogenetic and trait data, and has been shown to outperform other JSDM frameworks, particularly when modelling sparse species data (Norberg *et al.* 2019), which was the case in my arthropod data

4 MAIN RESULTS AND DISCUSSION

In this thesis, I showed that vegetated roofs in temperate and southern boreal climates harbour arthropods that typically occur in open dry habitats or are habitat generalists. The arthropod assemblages on roofs consisted mainly of mobile species using active and passive aerial dispersal strategies to reach the rooftops, accompanied by a few species that likely arrive with roof construction materials. The majority of arthropods collected from the roofs were common, native, widespread generalist feeders. A few species were classified as rare or endangered and one true bug species was considered exotic. The characteristics shared by typical roof fauna point to the importance of environmental filtering and dispersal constraints in community assembly of vegetated roofs: species that are poor dispersers do not reach the rooftops and those that have low tolerance to drought fail in establishing viable populations on roofs with shallow substrates and minimal plant care.

Vegetation was an important driver of abundance of the arthropod groups I studied (Fig. 5). Although in this thesis, its effect on species richness appeared weak, I found a vegetation imprint on the communities, as arthropod assemblages differed between succulent and meadow roofs (Fig. 6, **II**), which are common roof vegetation types in both boreal and temperate climates. Predictions from the IBT hold weakly as roof height and size were typically not important in explaining species richness and their effects on abundance were sometimes even the opposite to what I hypothesized based on the IBT. Furthermore, the landscape, described as proportions of potential source habitats and likely non-source habitats for roof fauna, shaped arthropod community composition but not richness, and local roof characteristics were more important in explaining abundances of individual species and taxa compared to landscape variables (**I**).

I found new roofs to accumulate species for at least three years after they were built, but species richness to remain constantly lower on

roofs compared to reference sites at ground level. I detected a shift in trait composition of roof communities, as the proportion of predators increased with time on roofs but not in the ground level sites and found the species' responses to roof height and size to differ between feeding groups (Fig. 7). Temporal patterns in roof communities indicated a non-random assembly process: with time the roofs became more similar to one another compared to their reference habitats at ground level.

4.1 MEADOW AND SUCCULENT ROOFS BENEFIT MOBILE SPECIES OF OPEN DRY ENVIRONMENTS

With data from beetles, true bugs, spiders and ants, I showed that non-irrigated vegetated roofs with low open vegetation mostly accommodate common species of open dry habitats, mobile pioneers, species with wide habitat tolerance and species that are generalist feeders. Data on habitat affinity in **Chapter II** imply that, especially for spiders, there is spill-over on roofs from other kinds of habitats, such as forests and wetlands, but it has low importance, as the abundant species were either associated with open habitats or had wide habitat tolerance. Typical species characteristics are in line with previous studies that also found vegetated roofs with shallow substrates and low maintenance to harbour open habitat arthropods, xerophilic and thermophilic species, and habitat generalists (Kaupp *et al.* 2004; Madre *et al.* 2013; Bergeron *et al.* 2018), supporting the idea of using vegetated roofs in mitigating the loss of open habitat species.

Comparison between arthropod communities on new roofs and in adjacent ground level sites (**III**) showed that roofs are colonized by species that are common in local ground level communities. Several true bug species that were frequently found on new roofs (**III**) were the same that I found to be common and abundant on older vegetated roofs in **Chapter II** (age 3–21 years). In addition, the most abundant spider and ant species on older roofs were also common on newly constructed roofs. Whether this is explained by high suitability of the studied roofs to these com-

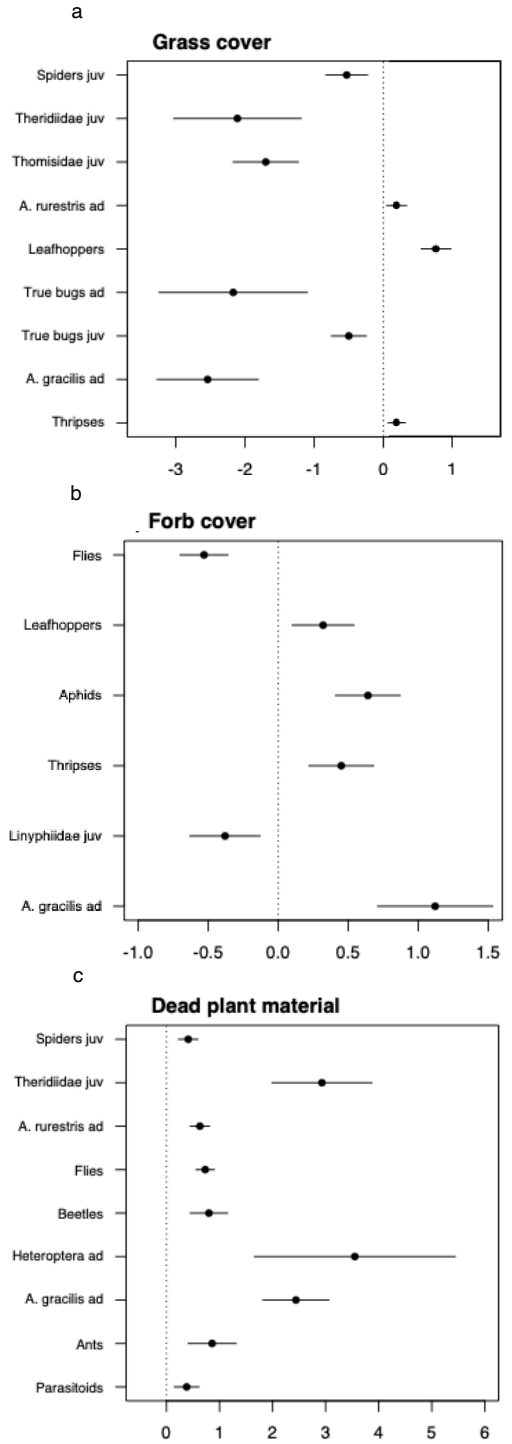

Figure 5. Abundance responses (model coefficients +- SE) of various arthropod taxa to grass cover (a), forb cover (b) and dead plant material cover (litter and standing dead plants) (c) in **Chapter II**. Juv = juveniles, ad = adults. Note that scales for x-axes are unique for each plot.

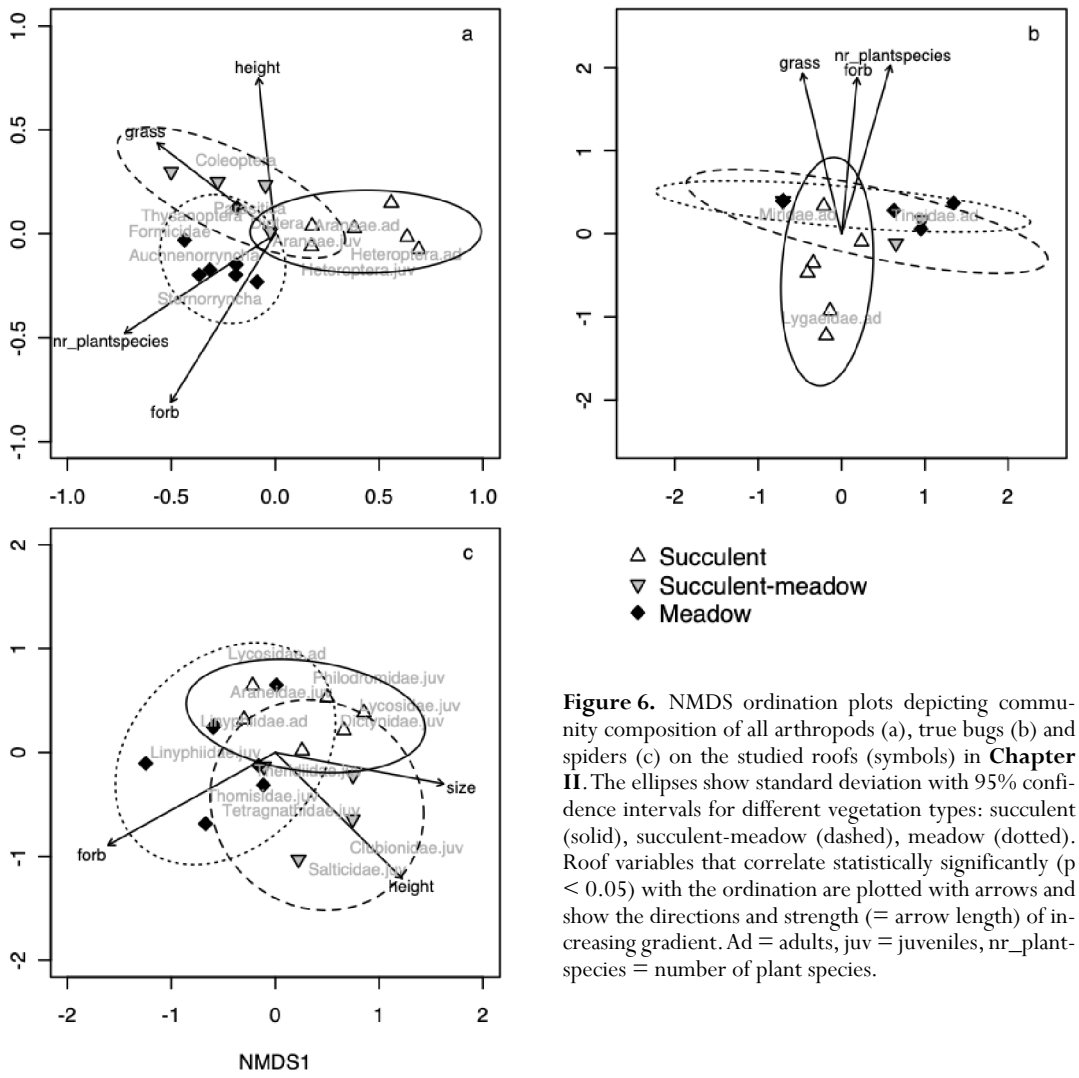

Figure 6. NMDS ordination plots depicting community composition of all arthropods (a), true bugs (b) and spiders (c) on the studied roofs (symbols) in **Chapter II**. The ellipses show standard deviation with 95% confidence intervals for different vegetation types: succulent (solid), succulent-meadow (dashed), meadow (dotted). Roof variables that correlate statistically significantly ($p < 0.05$) with the ordination are plotted with arrows and show the directions and strength (= arrow length) of increasing gradient. Ad = adults, juv = juveniles, nr_plantspecies = number of plant species.

mon species, or if their persistence is dependent on constant recolonization from ground level, cannot be inferred from empirical snapshot data, but would be an interesting question for further studies.

At coarse taxonomic levels, roof communities resemble ground level habitats: nearly all insect orders present at ground level are found on roofs (**III**) and even family richness of vegetated roofs may mirror arthropod communities at ground level (MacIvor and Lundholm 2011; Dromgold *et al.* 2020). In **Chapter III**, Blattodea (here only cockroaches) was the only arthropod order that was collected from ground level sites but not from roofs. As females of the collected species are wingless, the absence of Blattodea should reflect a dispersal barrier from vertical isolation. Furthermore, even though roof communities are unique in their trait composition, functional richness can be similar on roofs and ground level sites (Braaker *et al.* 2017), suggesting that the roofs correspond to ground habitats in ecosystem functioning. Yet, species richness remained constantly lower on young roofs compared to ground level communities (**III**). Also, the number of ant species was low (2 species), and spider communities were mainly dominated by a single

Linyphidae species on 3–21 years old roofs (**II**). The lower arthropod species richness of vegetated roofs compared to urban ground level open habitats is a typical phenomenon (Colla *et al.* 2009; Tonietto *et al.* 2011; Braaker *et al.* 2017, but see MacIvor and Lundholm 2011) and pinpoints to the importance of the additional filter of the roof environment for urban ground level fauna as a driver of community assembly. Even though the lower species richness on roofs compared to ground level have not been shown to affect the ecological functioning of roofs, it may decrease the stability and resilience of roof communities (Campbell *et al.* 2011) and reduce their value as conservation tools. Thus, understanding how spatial and biophysical roof characteristics are connected to species assemblages and applying solutions that promote species rich roofs remains important.

4.2 ROOF VEGETATION IS IMPORTANT

Results from **Chapters I and II** told roughly the same story even though they were conducted in different climates and focused on different taxa: arthropod abundance and community composition are connected to vegetation characteristics (Figs. 5, 6). As vegetation has a key role in shaping arthropod fauna, results from this thesis are only applicable to roofs with low, drought tolerant vegetation, whereas characteristics of arthropod fauna of roofs that have different vegetation, e.g., irrigated garden roofs with trees and shrubs, are likely different.

Responses to vegetation characteristics were taxon-specific but with most taxa showing positive association with forb and grass cover (**I**) or increase with forb cover but decrease with grass cover (Fig. 5a–b, **II**). Also, litter and other dead plant material had a positive effect on arthropod abundance (Fig. 5c, **II**). Forb and grass cover were always negatively correlated with succulent and moss cover and positively with plant species richness. Thus, the positive response to forb and grass cover is likely connected to an increase in resources for herbivores on meadow roofs compared with succulent and moss dominated roofs. Only a couple of the collected species are known to feed on succulents or mosses (**II**) and our succulent roofs had a modest diversity of herbivores as some herbivorous taxa were absent or occurred only in low numbers on succulent roofs (**II**).

In addition to providing resources for herbivores, the positive effect of forb and grass cover on arthropods may also be connected to an increase in plant biomass and habitat complexity. Increase in plant biomass further improves the amount of food resources available for herbivores and increase in habitat complexity increases opportunities to find microhabitats that provide, e.g. suitable foraging sites, and places to escape natural enemies (Siemann *et al.* 1998; Haddad *et al.* 2001, 2009; Langellotto and Denno 2004). As I did not measure plant biomass or habitat complexity of roofs, detailed patterns behind the positive connection between forb and grass cover and arthropod abundance remain unclear. Finally, the positive relationship between dead plant material and arthropod abundance (**II**) points to the importance of litter as a habitat component for arthropods. It provides shelter and food and can improve soil moisture, with positive effects on ground-dwelling arthropods (Uetz 1979; Ober and DeGroote 2011).

Vegetation characteristics were also important for predatory arthropods, but with partly conflicting results compared to herbivores. Similarly to herbivores, parasitoid (Hymenoptera: Apocrita: Parasitica) abundance showed a positive response to forb and grass cover and ant abundance was positively connected to substrate depth, a variable that had a strong positive correlation with forb and grass cover (**II**). Spiders were more abundantly caught on succulent and moss dominated roofs compared to roofs dominated by forbs and grasses (**II**). I did not measure habitat complexity but assume it to be positively connected with plant diversity: from personal experience, succulent roofs were simpler in regard to vegetation structure, measured as variation in plant height and the number of vegetation layers, compared to meadow roofs. Therefore, the result is in conflict with the prediction that plant diversity and habitat complexity have positive effects on predator abundance. The result is also opposite to earlier findings on spider abundance

patterns on different roof types in temperate climates (Brenneisen 2006; Madre *et al.* 2013). A possible explanation is lower food competition on succulent roofs compared to roofs that have deeper substrates: ants that excavate nests in substrate were rare on succulent roofs, but small Diptera species, which are important prey for various spiders, were abundant on both meadow and succulent roofs (**II**).

4.3 THE PUZZLING ROLES OF ROOF SIZE AND CONNECTIVITY

In contrast to what I hypothesized based on IBT, roof size and height did not explain arthropod richness, described as number of species. Abundance patterns of individually analysed taxa in relation to roof height and size were partly even opposite to what I hypothesized. In **Chapter I**, height was rarely important in explaining abundance patterns of individually analysed taxa, and in **Chapter II**, I found a predominantly positive connection between roof height and abundance of those arthropod taxa for which the roof height was an important predictor. Hence, vertical isolation appears to be a critical dispersal constraint for some arthropods, but species that are able to establish on roof tops are rarely negatively affected by increase in roof height: they seem to tolerate strong winds and exposure to sun and may benefit from decreased competition and predation on high roofs. However, my data did not include very high roofs (highest roofs in **Chapters I, II and III** were 22, 11 and 14 m, respectively), and above a certain threshold, vertical isolation and abiotic conditions may start to hinder arthropod dispersal, survival and reproduction.

Roof size and abundance were connected for various taxa, but with variation in the direction of responses (**I & II**). This may be explained by the small island effect (SIE). The area of my study roofs was typically small, particularly in **Chapters II and III.** Even in **Chapter I**, only the two largest roofs were over 1 ha in size, i.e. area that is often considered as a threshold for small habitats at ground level (Wintle *et al.* 2019), and the taxon-specific threshold area for SIE is typically even larger (Wang *et al.* 2018). Thus, features other than roof size seem more important for the studied arthropods (Lomolino 2000; Triantis and Sfenthourakis 2012), which in the case of vegetated roofs appear to be habitat quality, or vegetation (see previous section). Furthermore, the role of roof size for species richness is likely connected to microhabitat variation (Niemelä *et al.* 1996; Langellotto and Denno 2004). If the roof is constructed with uniform substrate composition and depth, has little variation in shading conditions nor much slope, increased roof size may not lead to an increase in microhabitat variation.

I showed that landscape features affect community composition and also abundances of some beetle species, but not species richness (**I**). According to Braaker *et al.* (2014), habitat connectivity and land cover types surrounding the roofs are important for highly mobile taxa (bees and weevils [Coleoptera: Curculionidae] in their study). Instead, community composition of less mobile taxa (spiders and carabids) were primarily shaped by local roof characteristics (roof age, size and vegetation characteristics). I did not observe a similar pattern: variation in species mobility was relatively low as shown in **Chapter I** – there were no wingless species, and taxa responding to land cover features included both winged and dimorphic species.

Beetle abundances in **Chapter I** were positively affected by open and semi-open green space in the immediate surroundings of vegetated roofs (within a 100 m buffer), and in **Chapter III**, ground level habitats close to roofs provided important sources for roof fauna. Yet, in **Chapter I**, the effect of potential source habitats in a larger area (400 m buffer) on beetle abundance was mainly negative and the effect of impervious surface was positive. According to my predictions from IBT, abundance should have increased with proportion of open and semi-open green space (i.e. potential source habitats) and decreased with proportion of impervious surface (i.e. uninhabitable matrix). Therefore, while my results supported the idea that open habitats in the immediate surroundings have a direct impact on roof fauna via providing sources for colonization, the landscape at large appears to affect the roof fauna indirectly. This indirect effect could relate to

decreased predation by insectivorous birds and bats in urban cores with little vegetation (Avila-Flores and Fenton 2005; Threlfall *et al.* 2016), but the topic requires further investigations.

To conclude, predictions about the role of roof size and connectivity from IBT do not seem applicable to arthropods on vegetated roofs. Blank *et al.* (2017) also failed to find strong support for predictions of IBT on vegetated roofs in their review on invertebrates. They argued that the reason might be limitations in available data: studies testing predictions of IBT on vegetated roofs are few and are based on low number of replications and variation in roof height is often low. Thus, the studies may lack power to observe statistically significant connections. Yet, as my results add to the number of studies failing to find strong support for IBT predictions in roof habitats, it seems that these spatial variables do not have an important role in shaping species richness of vegetated roofs, and that local habitat quality is a more important driver of arthropod communities on vegetated roofs.

4.4 TEMPORAL PATTERNS IN THE ROOF FAUNA

While succession in roof vegetation has been described in several studies (Emilsson 2008; Thuring and Dunnett 2014; Ksiazek-Mikenas *et al.* 2018; Aloisio *et al.* 2019; Jauni *et al.* 2020), temporal patterns in the arthropod fauna are less known. I did not find the order of species arrival, i.e., stochastic priority effect, to be important in community assembly of new vegetated roofs (**III**). Instead, roof communities started to resemble one another with time during the first three years after roof establishment. The increase in similarity may relate to high drought stress on the studied roofs, as abiotic stress should be positively connected with the strength of environmental filtering and to promote species similarity (Sommer *et al.* 2014), and/or to vegetation similarity.

Roof age is typically correlated with other biophysical roof characteristics, particularly vegetation (e.g., Madre *et al.* 2013; Ksiazek-Mikenas *et al.* 2018), which complicates the interpretation of results from space-for-time substitution studies on arthropods. On roofs where total vegetation cover increase with roof age (Ksiazek-Mikenas *et al.* 2018), there are likely positive effects on arthropod richness and abundance (Schindler *et al.* 2011; Salman and Blaustein 2018). Yet, also the dominance patterns in plant communities change with time: for example, Gabrych *et al.* 2016 reported an increase in forb and grass cover with roof age and substrate depth, whereas they found most succulents to decrease in cover with age, regardless of substrate depth. Also, the proportion of grasses may show a strong positive correlation with roof age (Kyrö *et al.* 2020). As vegetation quality strongly affects arthropod diversity, abundance and community composition (Siemann *et al.* 1999; Morris 2000; Joern and Laws 2013; Prather and Kaspari 2019), these temporal changes in roof vegetation should have complex community level effects on arthropods.

In my work, the effects of roof age on arthropod abundance and richness were variable. In **Chap-**

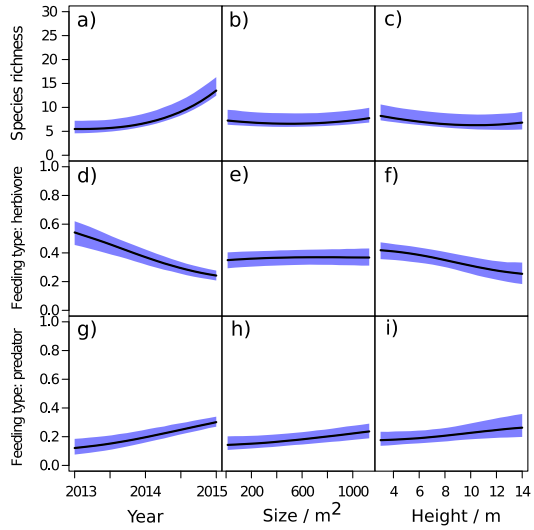

Figure 7. Predictions showing patterns in expected species richness (a–c) and fractions of arthropod juvenile feeding types (d–i) on vegetated roofs with time (first column), roof size (second column) and roof height (third column) in **Chapter III**. In addition to herbivores and predators, feeding type data include fungivory, detritivory, sanguivory and xylophagy, which were combined in one class (included in the intercept). Predictions are made at the level of an individual suction sample and confidence intervals are plotted as coloured areas.

ter I, beetle abundance mainly declined with roof age, but richness varied regardless of age. In **Chapter II**, true bug richness showed a negative response with age, while spider richness varied regardless of roof age. Also, age was, in general, unimportant in explaining abundance of different arthropod taxa and it had both positive and negative effects when remaining as a predictor in the models after model selection. Only in longitudinal data from recently established vegetated roofs (**III**) did species richness increase with age as expected (Fig. 7a), but due to a gap in the data for the second sampling in the first year's data (2013) the increase in species richness from 2013 to 2014 may have been less steep than expected in our predictions.

The varying effects of roof age on richness may be explained by a non-linear age-richness relationship. New roofs have plentiful ecologically open space for pioneer species and species richness increases with time. However, at some point, changes in vegetation (e.g., increase in the dominance of grasses) and an increase in competition and/or predation should start to limit the establishment of new species while simultaneously driving local extinctions and cause a hump-shaped rather than a linear relationship between roof age and arthropod richness. Yet, species richness gives only a narrow perspective on the ecological value of roofs: interesting questions for further studies would be, do arthropod communities differ in trait composition and/or in the proportions of stenotopic, rare and endangered species on roofs with varying age.

4.5 WHEN WE KNOW BETTER, WE DO BETTER: DESIGNING VEGETATED ROOFS FROM A HABITAT PROVISION PERSPECTIVE

Independent of the main reason for building vegetated roofs, which may be other than habitat provision, roofs with a substrate layer are always colonized by plants and animals. Consequently, every vegetated roof is a habitat patch, regardless of its primary purpose. As shown in this thesis and other studies on vegetated roof arthropod fauna, roof design has an important role in the ability of the colonizing species to establish viable populations (Madre *et al.* 2013; Braaker *et al.* 2014; Pétremand *et al.* 2018). Hence, if we wish to use vegetated roofs as conservation tools to support a rich arthropod fauna and rare/endangered species, they need to be designed from a habitat provision perspective.

Thus far, the most encouraging results from habitat provision with vegetated roofs are from the city of Basel where beetle and spider species of conservation interest have successfully established on roofs that are specifically designed to resemble local river bank habitats and railway sidings (Kaupp *et al.* 2004; Brenneisen and Hänggi 2006; Pétremand *et al.* 2018). In Basel, regulation even obligates the design of vegetated roofs to support flora and fauna typical for the area. In addition, the use of local soil is promoted as it is considered as a potentially critical element to allow the establishment of (local) stenotopic arthropod species adapted to particular soil properties (Brenneisen 2006).

In this study, species of conservation concern were collected only on roofs in Basel (**I**). In the other study area, Helsinki, where most vegetated roofs have primarily been designed for landscaping and stormwater retention and have artificial substrates, no endangered or threatened species were found. The scarcity of rare or endangered species and specialist on the roofs reflects, on one hand, the characteristics and limitations of source fauna in urban ground level habitats (McIntyre *et al.* 2001; McKinney 2006; Piano *et al.* 2017), but on the other hand, points to a need to design vegetated roofs specifically from a habitat provision perspective to increase their contribution to urban biodiversity. For instance, if the local or regional ground level arthropod fauna includes mobile oligophagous herbivores, planting their preferred food plants on roofs and targeting management to support them could improve the ecological value of roofs. Also, as conservation assessments for invertebrates are largely lacking compared to vertebrates (van Swaay *et al.* 2011; Cardoso *et al.* 2011), it is possible that vegetated roofs support declining species, which are not yet recognized as conservation concern.

Given the low support for predictions from the IBT in roof habitats, the value of vegetated roofs for arthropod conservation can be improved by focusing on the features of roof vegetation and substrate and improving land cover properties for target taxa in the immediate surroundings of the roofs, regardless of roof size and height. Forb and grass dominated meadow roofs support higher herbivore richness and abundance compared to succulent roofs (Madre *et al.* 2013). Yet, succulent roofs have distinct arthropod communities that may include unique species (Kyrö *et al.* 2020), and therefore can contribute positively to beta diversity. Hence, planting roofs with diverse native vegetation, favouring forbs and mixing succulents, grasses and mosses with them should be promoted. In addition, as it is not merely the living plants that matter for arthropods, but also litter, unnecessary manicuring of roof vegetation needs to be avoided. Instead, estate owners should be encouraged to allow for the accumulation of a litter layer, even if there might be aesthetics-based pressure to remove dead plants, especially on roofs that are accessible for recreation.

Even though roof size did not explain arthropod richness, applying roof designs that allow habitat variation to increase with roof size, i.e., ensuring variation in substrate depth and composition and planting diverse selection of plants, remains important. The effects of small-scale habitat variation in epigeal arthropods have not been studied on vegetated roofs but the increase in microhabitats has often a positive effect on species richness (Guido and Gianelle 2001; Lengyel *et al.* 2016). Furthermore, roof size should be positively connected to stability of arthropod populations as in small habitat patches, populations are more prone to extinctions compared to large patches (Hill *et al.* 1996). Also, on large roofs it is easier to provide conditions that allow the target species to successfully complete its life cycle. Thus, particularly if the roofs are designed for the conservation of a certain species, large roofs should be favoured to decrease the probability of stochastic extinctions. Very small roofs, such as bus stop roofs, could in turn function best as foraging sites and stepping-stones and connect the urban green space for arthropods that use active aerial dispersal strategies, such as bees. The ecological value of small roofs may increase if several small roofs designed for the same target taxa are located close to each other and form a network (Baguette *et al.* 2013). In addition, although increase in roof height is a minor issue for aerial dispersers, improving vertical connectivity of roofs with green ramps, or even with green walls for species that are able to move vertically in the vegetation, may enable the colonization of species and individuals that lack aerial dispersal strategies (Fig. 8).

As the urban ground level green space surrounding the roof provides an important source for the roof's arthropod community (Braaker *et al.* 2014; Kyrö *et al.* 2018; Dromgold *et al.* 2020, **Chapter III**), to have wildlife to thrive on a city, it needs to flourish also in the city. Ideally, the design of roofs and the closest ground level habitats should go hand-in-hand. If the ground level green space includes open habitats of high ecological value, mimicking these local habitats on roofs should be prioritized. Instead, when the ecological value of local ground-level green space is low, improving ground-level habitat is also important. For example, in areas where the closest source habitats are intensively managed lawns, converting these to meadows with native plant species and planting the roofs with similar vegetation benefits also arthropod conservation.

The roofs in Helsinki lacked species assessed of conservation concern but two nationally rare snail species and a true bug species have been collected from them (Páll-Gergely *et al.* 2014; Kyrö *et al.* 2020). These species were deemed as likely hitchhikers arriving in imported plant materials. They appeared to be able to establish viable populations on roofs and at least the true bug species had likely dispersed from roofs into ground level. This is both encouraging and alarming: accordingly, the roofs may even function as source habitats for metapopulations, but as the rare species were exotics, our observations reveal a risk of vegetated roofs as sources for unintentional species introductions with poorly forecasted, potentially negative consequences on local ecosystems (Goodenough 2010; Jeschke *et al.* 2014).

Lastly, to evaluate the success of vegetated roofs as habitat templates, we should define clear, measurable goals for them (Williams *et al.* 2014). Possible goals could be to increase the amount and improve connectivity of local open habitats, especially those of high conservation interests, to provide feeding and nesting sites for pollinators and to support specific species. Given the typical characteristics of vegetated roofs that do not require frequent management, roofs are particularly suitable for conservation efforts of sun exposed dry habitats and their associated species. In Finland, such habitats include, for instance, rocky and sandy meadows, ruderal areas and sandy eskers (From 2005). Importantly, involving ecologists in the planning process of new vegetated roofs to recognize best local target habitats for roofs and to assure that the roof design carefully mimics them should be encouraged when using vegetated roofs as conservation tools.

4.6 CONCLUSIONS AND FUTURE PERSPECTIVES

My thesis adds to the growing amount of knowledge on vegetated roofs' arthropod fauna and provides insights from the processes that shape arthropod communities on roofs. I found urban vegetated roofs with drought-tolerant plant assemblages to contribute to habitat provision for mobile generalists and species that associate with dry open habitats. These typical characteristics were shared among the most common species of different arthropod taxa (beetles, true bugs, ants and spiders) in temperate and boreal climates. Habitat quality was more important in explaining arthropod richness and abundance than roof size and the effect of vertical isolation was partly contradictory to what I predicted based on IBT. Accordingly, walls set a dispersal barrier for poorly mobile species but those that fly or rain on roofs are insensitive to an increase in roof height or even profit from landing on high roofs. Also, although abundance and species richness varied regardless of roof size, patch area should be positively connected to community stability (Hill *et al.* 1996; Bonte *et al.* 2002), which is an important aspect to consider when planning vegetated roofs for species conservation.

Similarly to Pétremand *et al.* (2018), I found vegetated roofs that are not primarily designed to support biodiversity to often have low spe-

Figure 8. Connectivity of vegetated roofs, particularly for species that lack aerial dispersal strategies, could be improved with vegetated ramps and walls. Examples of vegetated ramps and walls: an old turf-roof hut in Northern Finland (Siida museum) (a), modern vegetated roof that is part of a sheep pasture (b), vegetated wall created by creepers that are self-attached to the building face (c), and modern vegetated wall with climbers attached to wire ropes (d). Photos: Kukka Kyrö.

cies richness and lack species assessed to be of conservation concern. I also found support for the expectation that roof habitats can contribute to conservation of endangered species with a preference for dry and xeric habitats if suitable conditions are created (Brenneisen 2006; Kadas 2006; Pétremand *et al.* 2018). For most taxa, diverse meadow vegetation was superior compared to monotonic succulent-moss roofs. Thus, my results point to an importance of cherishing plant diversity on roofs that are hoped to provide habitats for rich arthropod fauna.

The relative importance of local habitat characteristics and the landscape on arthropods in urban environments depends on studied taxa and their traits, particularly dispersal capacity (Braaker *et al.* 2014; Burkman and Gardiner 2014; Peng *et al.* 2020). Thus, we should be careful about generalizations on their roles, but my results are in line with studies that stress the importance of local habitat characteristics for arthropods in urban areas (Philpott *et al.* 2014; Otoshi *et al.* 2015), and point to a key role of roof design for the value of vegetated roofs as arthropod habitats. In addition to diverse vegetation, habitat elements known to benefit various arthropods of conservation concern in ground-level habitats, such as deadwood, areas of bare, sandy substrate, stone piles and water elements, are frequently applied on roofs to increase their ecological value. Encouragingly, preliminary discoveries support their assumed benefits (Nash *et al.* 2016). Yet, to provide strong evidence-based tools for roof designers, systematic studies on the contribution of additional habitat elements to arthropod richness and species of conservation concern on different kinds of vegetated roofs are still required.

My results concerning community assemblies of new vegetated roofs showed the roofs to become more similar with time. I interpret this as an indication of a potentially strong importance of deterministic environmental filtering that may relate to vegetation features and to high tolerance to drought stress required for species that successfully establish populations on roofs with shallow substrates. Three years is a rather short time frame and furthermore, in this case, data were largely missing for one out of six sampling occasions, which made interpretations of temporal patterns difficult. It would be interesting to determine if the communities remain more similar to each other than to nearby source habitats at ground level when they get older. Varying results of the effects of age on abundance and richness of the studied arthropod taxa also underline the need for long-term studies. As the colonization routes to new vegetated roofs include hitchhiking with construction materials, these longitudinal surveys should ideally start from nursery gardens.

Although I found deterministic processes to be likely important in shaping arthropod communities on vegetated roofs, further studies on the relative roles of stochastic and deterministic processes in vegetated roof communities are still needed to shed light on the mechanisms structuring roof communities. Given the harsh environmental conditions on roofs, a process based on environmental filtering and differences in species niche preferences, i.e. the species sorting paradigm in metacommunity theory (Leibold *et al.* 2004), may play a significant role in vegetated roof communities. However, because other mechanisms, particularly competition, can generate similar community patterns with environmental filtering, experimental data are needed to reliably evaluate the importance of environmental filtering on vegetated roofs (Cadotte and Tucker 2017). Furthermore, as high dispersal ability is a typical feature of roof fauna, mass effects, i.e., a process that allows species to persist in unfavourable sink habitats – because they receive immigrants from source habitats that have suitable environmental conditions (Mouquet and Loreau 2003) – may also explain much of the observed community patterns on roofs. Also the two remaining metacommunity paradigms, patch dynamics and neutral model (Leibold *et al.* 2004), are potentially important on roofs. Frequent environmental disturbances, such as droughts, and demographic stochasticity possibly linked to, e.g., small roof size, are considered typical for vegetated roofs. They could drive stochastic extinction patterns associated with the patch dynamics paradigm, in which habitat patches are assumed to be similar in quality and species regional coexistence is per-

mitted by colonization-competition trade-offs. In addition, relatively low variation in dispersal ability and habitat affinity of roof fauna may indicate that neutral processes, in which species are assumed to have equivalent niche preferences, dispersal and competitive abilities, also play a role in structuring roof communities for some taxa.

Closest open habitats at the ground-level were important sources for the arthropod fauna on roofs. Hence, vegetated roofs should be designed as elements of the existing network of open habitats by, e.g., mimicking local habitats with high ecological value. Based on my results using the beetle data, the larger landscape may have rather indirect effects on arthropods, possibly via changes in ecological networks. To my knowledge, ecological networks, such as food webs or competitive interactions, have not been considered in studies on vegetated roofs arthropods. Here lies an important knowledge gap: biotic interactions can have an important role in community assembly (Kraft *et al.* 2015) and may explain much of the variance left unexplained when modelling species abundance or occurrence as a function of local and landscape variables. In addition, describing food webs on roofs and comparing them to urban ground level habitats, could provide valuable information on the functioning of roof ecosystems (Thébault and Loreau 2006; Hines *et al.* 2015) and push forward our understanding of these artificial habitats.

5 ACKNOWLEDGEMENT

After an unexpectedly long adventure with this thesis, I am overwhelmingly happy to write these lines to thank everyone who have helped and supported me on the way.

First and foremost, I thank my supervisors Susanna Lehvävirta and Johan Kotze. Susanna, I could not be more grateful for the endless amount of support and guidance over the years! I also hugely appreciate the way you challenged my thinking and pointed out so many times that things, which may appear simple are often not. Johan, a million thanks for stepping in, helping whenever needed and for being the calm, kind and cheerful person you are.

Ferenc Vilisics, thank you so much for introducing me to the wonderful world of invertebrate research and for all the time and effort you put in my guidance in the beginning of this journey. Special thanks for all the fun memories from those days when we travelled around Helsinki and vacuumed the roofs.

Thank you, Jyrki Muona, Kalle Ruokolainen and Timo Vuorisalo for your support as members of my thesis advisory committee. I value your advice and all the encouraging words I received from you. Thank you, Heikki Setälä, for supporting me in the beginning as an advisory committee member and for all the help later on. In addition, I am deeply grateful for the chance I got to share thoughts on vegetated roofs and their potential role in species metapopulations with the fifth original member of my thesis advisory committee, Ilkka Hanski.

I am grateful for all the co-authors I worked with during these years. Stephan, Magda, Alexander, Sanja, Elöd, Timo, Tuomas and Eero: thank you for your invaluable contribution! Extra thanks to Stephan, for organizing a roof tour in Switzerland and for sharing your extensive knowledge of vegetated roofs.

I am very grateful to Sheila Colla and Atte Komonen for accepting the invitation to review my thesis. Many thanks for all the valuable feedback I received from you. Thank you, Karl Evans, for agreeing to be my opponent.

For funding my work, I thank University of Helsinki Research Foundation, Maj and Tor Nessling Foundation, Uudenmaan liitto, the Department of Environmental sciences in the University of Helsinki, YEB Doctoral School, Kuopion Luonnonystäväin yhdistys, Oskar Öflunds Stiftelse, *Societas pro Fauna et Flora Fennica*, Suomen Hyönteistieteellinen Seura, and Arkta Reponen Oy. In addition, I thank Luova Doctoral Programme for travel grants.

Many thanks to the brilliant Fifth Dimension-gang. Marja, Taina, Kiiki, Gosia, Long, Juhamatti, Xi, Miia, Marleena, Ville and Iiris, I have enjoyed a lot doing research with strong practical and applied implications with you. Thank you for everything but the karaoke nights!

Thank you, Henri, for joining our group first as an intern and later as a master's student. It was super nice to work with you! Also, many thanks to Isabella, Giulia, Elina, Jutta and everyone who helped me in the field or in the lab even a day or two. Without you, it simply would not have been possible to conduct this research.

Thank you, Jari Niemelä for warmly welcoming me in the in the Urban Ecology Research Group. Thank you also Jarmo, Kati, Vesa, Kaisa, Silviya, Stephen, Anna, Joel and Yuan. It was wonderful to share a corridor for a few years with people who are passionate about urban nature.

Huge thanks to everyone in the Spatial Foodweb Ecology Group for adopting me for a while and sharing your expertise on metabarcoding and Hmsc. Special thanks for all the cheerful lunch and coffee breaks – you truly are experts in those, too! Also, extra thanks to Tuomas for all the help and trivia knowledge about invertebrates and for the layout of this book.

Thank you, Esa Tulisalo, for helping with practical issues (which was not little) and for your good humour and endless patience during the years. Thank you, Jukka Kaario, for patiently helping with various administration issues. Also, thank you very much, Karen Sims-Huopaniemi, for helping me whenever I got lost in the jungle of requirements related to doctoral studies.

Very many thanks go to all my wonderful and amazing friends. I have met most of you as a biology student or when doing field work or while working in biological field stations, and I simply cannot think of anything more fun than exploring and enjoying the woods, meadows and fjells with you!

Suuri kiitos Maritalle ja Hannulle tuesta, avusta ja elämänviisauksista. Kiitos Sannalle, Sinille ja Johannekselle hauskoista lomapäivistä mm. Vähiksellä ja Savossa. Kiitos parhaalle isoveljelle, Mikolle, sekä Ninalle, Siirille ja Veeralle juhlapyhien jakamisesta ja arjen kyläilyistä.

Kiitos äidille ja isälle kodista, jossa ei ollut koskaan liikaa kirjoja. Kiitos metsiin, hiihtoladuille ja hillasoille viemisestä. Valtava kiitos äidille loputtomasta tuesta, kannustuksesta ja myötäelämisestä, kulttuurin pariin tuuppimisesta ja kierrätysnikseistä. Isä, tiedän että olisit ollut ylpeä, kun lopulta sain tämän kirjan valmiiksi. Paljon tärkeämpää oli kuitenkin aika, jonka ehdit viettää lastenlastesi kanssa.

Lopuksi kiitos tärkeimmille. Kiitos Jaakolle kaikesta tuesta ja rakkaudesta. Kiitos Pinjalle heppajuttujen jakamisesta. Ailo ja Aslak: kotiovelta avautuva maailma on kerrassaan huikea seikkailtavaksi kanssanne!

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